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REVIEW

Surplus killing by pumas *Puma concolor*: rumours and facts

Mauro LUCHERINI* *Grupo de Ecología Comportamental de Mamíferos, Laboratorio de Fisiología Animal, Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur – INBIOSUR (Instituto de Investigaciones Biológicas y Biomédicas del Sur), CONICET, San Juan 671, Bahía Blanca 8000, Argentina. Email: lucherinima@yahoo.com*

Maria de las Mercedes GUERISOLI *Grupo de Ecología Comportamental de Mamíferos, Laboratorio de Fisiología Animal, Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur – INBIOSUR (Instituto de Investigaciones Biológicas y Biomédicas del Sur), CONICET, San Juan 671, Bahía Blanca 8000, Argentina. Email: mariadelasmercedesguerisoli@gmail.com*

Estela M. LUENGOS VIDAL *Grupo de Ecología Comportamental de Mamíferos, Laboratorio de Fisiología Animal, Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur – INBIOSUR (Instituto de Investigaciones Biológicas y Biomédicas del Sur), CONICET, San Juan 671, Bahía Blanca 8000, Argentina. Email: eluengos@gmail.com*

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*Correspondence author

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ABSTRACT

1. Surplus killing (i.e. predation in which predators kill more prey than necessary to satiate their hunger) appears to be widespread in carnivores and has the potential to exacerbate human–carnivore conflict. Nevertheless, little is known about the frequency of surplus killing or about its impact on livestock.
2. We review the information available on surplus killing by pumas *Puma concolor* and use data from central Argentina to quantify its impact on ranching and to analyse both its causes and its implications for puma–human conflicts.
3. We reviewed 73 publications and found nine mentions of surplus killing events from six countries. The sheep was by far the most commonly affected livestock species. In central Argentina, surplus killing was reported by 25–33% of the ranchers. In this region, the number of livestock killed during each event ranged from seven to 160 (median = 23) for the literature reports and from two to 70 (median = 7) in the records we personally collated. The number of individual animals killed per event was greater for interview-based second-hand reports than for first-hand reports and verified events.
4. Our results indicate that although surplus killing by pumas is uncommonly reported in the literature, it may be locally recurrent. Although surplus killing may be overestimated in interview-based reports, it can produce significant losses for sheep and goat ranchers, may strongly exacerbate puma–human conflicts, and should be considered in puma–human conflict mitigation strategies.
5. Ranchers typically attributed surplus killing to female pumas teaching kittens to hunt. However, there is little evidence supporting this interpretation. Surplus killing by pumas may be more likely to occur in situations where the predator's 'normal' hunting sequence is disrupted by the accessibility of large numbers of easy prey. Confinement, stormy weather and poor antipredator behaviour may favour the occurrence of surplus killing events on livestock.

INTRODUCTION

Human–carnivore conflict is a crucial global conservation issue. This conflict is often expressed through the economic costs carnivores impose on rural communities through predation on livestock, and the resulting 'preventative' or retaliatory killing of those carnivores (Treves & Karanth 2003, Graham et al. 2005, Berger 2006). Although the – actual or perceived – economic loss caused by predator attacks is treated as one of the main drivers of retaliatory killing, a person's reaction to depredation is a complex phenomenon, affected by a number of societal, cultural and behavioural factors (Loveridge et al. 2010, Dickman et al. 2013, Treves & Bruskotter 2014). The perception of risk can be more important than actual losses in shaping local people's attitudes towards carnivores (Naughton-Treves et al. 2003). Thus, surplus killing (i.e. predation in which predators kill more prey than necessary to satiate their hunger; Kruuk 1972) of livestock has the potential to exacerbate human–carnivore conflict, not only because it can escalate the effect of depredation on farmer livelihoods (e.g. Sangay & Vernes 2008, Muhly & Musiani 2009, Rigg et al. 2011), but also because it can aggravate pre-existing negative perceptions of predators (Kruuk 2002, Dickman et al. 2014).

Surplus killing (abbreviated as SK) is considered widespread in mammalian carnivores and has been a research subject from as early as the 1970s (e.g. Kruuk 1972, Bjärvall & Nilsson 1976). Kruuk (1972), in his seminal review on this topic, hypothesised that whereas killing and satiation is expected to inhibit the searching behaviour that leads to killing, continued killing (i.e. the behaviour occasioning surplus killing) at the same site is less likely to stop if other prey are still easily available. Such a situation is unlikely to occur in the wild but is frequent among domestic species, particularly those found in holding facilities made of low-quality materials. Nevertheless, the mechanisms triggering this behaviour are poorly understood. Few researchers, except for those studying wolves *Canis lupus* (e.g. Gazzola et al. 2008, Muhly & Musiani 2009), have analysed how frequently these events occur and how significant an impact they have on wildlife (Short et al. 2002) and livestock. Studies on livestock attacks by wolves showed that SK events tend to be rare but may nevertheless cause severe losses (Ciucci & Boitani 1998, Gazzola et al. 2008, Iliopoulos et al. 2009).

Like most large cats, the puma *Puma concolor* is a globally iconic but locally problematic carnivore (Inskip & Zimmermann 2009). Livestock predation by pumas is documented throughout the American continent (e.g. Torres et al. 1996, Soto-Shoender & Main 2013, Zarco-González et al. 2013, Ohrens et al. 2015, de Souza et al. 2018), and preventive sport hunting and retaliatory killing are the typical responses in North America and Latin America, respectively (Peebles et al. 2013, Guerisoli 2018).

Although it is known that pumas engage in SK throughout their large geographic range (Shaw et al. 2007, Murphy & Macdonald 2010, Ruth & Murphy 2010, Walker et al. 2010), we were surprised by the number of SK accounts reported by local ranchers when we started collecting information on puma–livestock conflicts in central Argentina (Guerisoli et al. 2017).

Here, we review the information available on SK in pumas, to understand the prevalence of this phenomenon over the puma's geographic range. Additionally, we use both published and unpublished data from a human-dominated rangeland of central Argentina to quantify the impact of SK on ranching activities, separate myth from reality surrounding the SK phenomenon, and reveal the potential impacts of SK on the management of puma–human conflicts.

METHODS

For this review, we defined SK events as those predation events in which two or more prey individuals were killed, but not consumed (Khorozyan et al. 2017). We reviewed two distinct sources of data for information on SK events attributed to pumas: 1) a database of publications obtained through a literature search; and 2) an original database of puma depredation events from central Argentina (Guerisoli et al. 2017). To construct the first database, we retrieved peer-reviewed English and Spanish language scientific articles and book chapters through Google Scholar and the International Union for Conservation of Nature's Species Survival Commission Cat Specialist Group Digital Library (http://www.catsg.org). As search words, we used the combinations of the common names of *Puma concolor* (i.e. puma, cougar, mountain lion and panther) with the words 'surplus killing', 'multiple killing' (Kossak 1989), 'excessive killing', 'diet', and 'food habits'. Additionally, we collected publications that matched our criteria by reviewing the literature cited in the articles and chapters from our search that seemed relevant (snowball sampling; Goodman 1961). Finally, we searched for additional reports of SK by thoroughly reviewing the literature database that we had previously created for a global review on puma–livestock conflict (Guerisoli 2018).

The second database we used to search for evidence of SK was originally constructed for a study that aimed to characterise puma depredation in the Espinal ecoregion of southern Buenos Aires Province, Argentina (Guerisoli et al. 2017). This study was based on 213 semi-structured interviews with cattle and sheep ranchers and 17 surveys of puma depredation sites that we personally conducted over an area of 23630 km^2 from 2007 to 2015 (see Guerisoli et al. 2017 for a detailed description of the methodology). Puma kills were identified by the presence of tooth (canine) marks on the prey's throat, by the marks of claws on the prey's back, by the presence of vegetation covering the carcass and/or by the dragging of the carcass.

In the literature search, we found nine papers in which SK by pumas was described (see Results), but detailed quantitative information was included in only two of these (De Lucca 2010, De Lucca & Nigro 2013). Because these two studies were conducted in central-eastern Argentina, we used the information they provided and information from our own database of interviews to characterise the impact of SK events in this specific region quantitatively. Ranching is the main economic activity in this region. Livestock include both cattle and sheep, and husbandry methods vary from intensive to extensive. Ranches vary largely in size and ranchers owing smaller herds tend to use more intensive grazing practices.

Because local people may inflate damage caused by wildlife (Naughton-Treves 1998, Kusler et al. 2017), we used a Kruskal–Wallis nonparametric ANOVA to assess if the number of animals killed by pumas during SK events was affected by the type of information source (i.e. personally verified cases, first-hand reports and second-hand reports).

RESULTS

The literature search returned 73 publications from 14 of the 23 countries where pumas occur; nine publications (12%) included original mentions of SK events. Only two (22%) of these mentions originated from direct observation by the authors, five (56%) were reports from ranchers. In two (22%) cases, the authors did not clarify their source of information. Sheep were the prey affected by SK in the majority of cases (73%), whereas attacks on cattle (calves), goats and pigs were rare (9% each). SK events were reported in Argentina (e.g., De Lucca 2010, Walker et al. 2010), Brazil (Mazzolli et al. 2002), Chile (Franklin et al. 1999, Murphy & Macdonald 2010), Costa Rica (Bustamante et al. 2014), Peru (Deustua Aris et al. 2008) and the USA (Shaw et al. 2007).

In the two published studies where quantitative information on SK events was included (De Lucca 2010, De Lucca & Nigro 2013), sheep and cattle ranchers (n = 70) from the lowlands of central-eastern Argentina were asked to report any depredation event they could remember. Almost one-third (33%) of ranchers reported SK by pumas; 22 cases affected sheep and only one involved cattle (calves). The number of livestock killed during these attacks ranged from seven to 160 (median = 23, IQ range: 13–50).

In the database we personally collected, SK records comprised 22 interview-based reports and five surveys of predation sites. Because our interviews had not been specifically designed to collect data on SK, we could not accurately calculate the frequency of SK reports; however, we estimated that SK was reported by approximately 25–30% of interviewees. Consistently, the five surveys where SK took place represented 29% of the total number (n = 17) of puma attacks we personally assessed. When all our records were pooled, 26 of the 27 cases affected sheep; in the remaining attack, three horses (foals) were reported killed. The median number of livestock killed during the attacks was seven (IQ range: 4–25) and ranged from two to 70 individuals, but 10 or fewer individuals were killed in 70% of the cases. The number of animals killed per event was smaller (Mann–Whitney U test: U = 57.5, P = 0.026) than that reported in the two previous studies from the same region (De Lucca 2010, De Lucca & Nigro 2013).

When the information was separated by type (i.e. verified field surveys, first-hand reports, second-hand reports), the number of sheep reported killed was greater in interview-based second-hand reports (median = 70, range: 50–160 individuals) than in first-hand reports (median = 12, range: 2–60 individuals) and the depredation events we personally verified via field surveys (median = 4, range 2–36; Kruskal–Wallis non-parametric ANOVA: H = 19.71, P = 0.0001; Fig. 1). All information sources indicated that most of the attacks affected adult sheep, but lambs were also frequently killed.

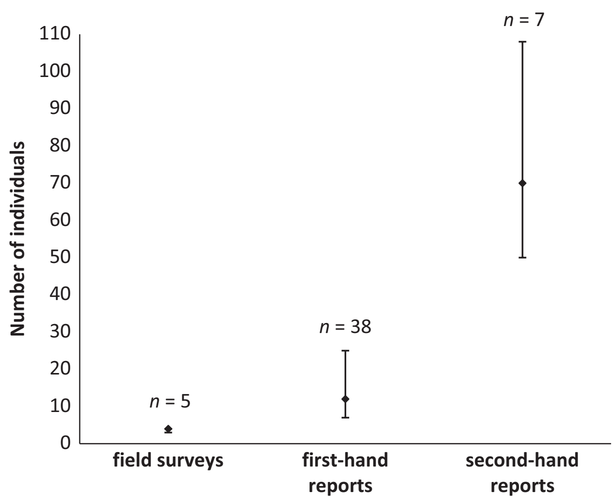

Fig. 1. Numbers (median ± IQ range) of individual livestock reported to have been killed in surplus killing events by puma *Puma concolor* in the rangelands of central Argentina. Based on their source, data are divided into verified field surveys, first-hand reports and second-hand reports. Sample size is also reported.

DISCUSSION

A potential caveat that may affect our results is related to our definition of SK. It could be argued that in the events where two individuals are killed, pumas may be able to cache them and return to them until they are totally consumed (especially if the prey body size is small), so such predation should perhaps not be described as SK. However, our database included only two cases where two sheep were predated, and we decided to include them because only small portions of these sheep were consumed.

Our review of the literature indicates that SK by pumas is relatively uncommon throughout this felid's geographic range. However, SK appears to be locally recurrent, occurring in 25–33% of the ranches in the area where we had the opportunity to quantify its incidence. We suggest that these results are not irreconcilable. We found that SK appears to affect primarily small livestock and can be related to extensive livestock grazing, so it is not surprising that it was not recorded in the areas where ranchers primarily raise cattle. It is also possible that authors do not mention SK in their publications because they do not consider it to be important or because they are unsure of the reliability of evidence on SK. However, it cannot be ruled out that both the frequency of occurrence and the incidence of SK are inflated in ranchers' reports. It has been noted that SK events can generate a 'hyper-awareness' of risk (*sensu* Dickman et al. 2014) in local people, by becoming stories that tend to be widely recounted for years (Kruuk 2002, Dickman et al. 2014). A detailed examination of our data supports the hypothesis that interview-based reports may overestimate the effect of SK. Although the number of SK attacks we personally verified was small, we found that the number of animals killed in each of these events was approximately one-fourth the number reported in interviews. This supports the hypothesis that interview-based reports may overestimate the effect of SK, especially for those events not directly obtained from the affected person, which is the sample that was likely to include only the most memorable events and that was more susceptible to overstatement. These results are also in agreement with the observation that local informants may overestimate the presence of conflictive and charismatic species, such as the puma (Caruso et al. 2017).

SK events may be distorted by word-of-mouth transmission of information. The most frequent explanation for SK given by local ranchers in our study area was that it was caused by female pumas teaching their kittens to hunt. This explanation was also recorded in Chile (Murphy & Macdonald 2010), Brazil (Mazzolli et al. 2002) and Florida, USA (Pienaar et al. 2015). Females of many felids, including pumas (Elbroch & Quigley 2013), are known to deliver live prey animals to their offspring and let them practice how to subdue and kill them (Caro & Hauser 1992, Kitchener 1999). However, the typical context where SK on livestock takes place (sheep herds in a corral) does not seem suitable for this type of learning experience. In fact, the context is much more in accordance with the mechanism that has been used to explain SK: it occurs specifically in unusual situations where the 'normal' hunting sequence is disrupted when the predator is confronted with many easily caught prey (Kruuk 1972). It was not uncommon to hear ranchers in our study area mention that the largest SK attacks occurred during stormy nights, when weather conditions appear to reduce the antipredator defences of prey (Kruuk 1972, Linnell et al. 1999). Although some evidence indicates that primarily male pumas are implicated in SK (Linnell et al. 1999), it is possible that females with young are most likely to risk entering corrals because of their greater energetic demands. Observations of tracks of an adult in the company of a young puma in SK events may have resulted in the explanation commonly adopted by local ranchers. The meagre evidence available suggests that SK in pumas may be a result of individual specialisation (Ross et al. 1997, Pienaar et al. 2015).

It has been suggested that sheep may be especially susceptible to predation by large carnivores because of their comparatively small size and their poor antipredatory behaviour, a side effect of the domestication process (Hansen et al. 2001). Indeed, they were by far the most common prey in the SK reports we collated. However, sheep are not the only livestock species that can be strongly affected by SK events; we recorded multiple predation events by puma, particularly on goats but also on pigs, horses (foals) and cattle (calves).

We surmise that confinement of livestock, stormy weather and poor antipredator behaviour may collectively create the conditions favouring SK of livestock by pumas in rangelands. Similar situations may encourage SK in other large cats living in similar environments (e.g. the Eurasian lynx *Lynx lynx*, leopard *Panthera pardus*, and snow leopard *Panthera uncia*).

Implications for conflict management

Although the true financial damage caused by puma SK attacks may be overestimated, it is clear that: 1) in some locations, SK may be a likely event for farmers, at least for those breeding sheep and goats; and 2) it can cause significant levels of temporarily concentrated losses. Similar to what has been observed in wolves (Muhly & Musiani 2009), SK is thus likely to significantly affect the perception of pumas by local people, not only because of the actual damage pumas cause, but also because of the fear and outrage that SK events generate. In turn, strongly negative perceptions may considerably decrease human tolerance and exacerbate conflict. In support, severe depredation events endured by a relatively small number of individuals appear to have a stronger influence on livestock producers' perceptions of depredation risk and losses than the average depredation (Agarwala et al. 2010, Pienaar et al. 2015), and produce intolerant reactions by the entire community (Lehmkuhler et al. 2007, Guerisoli et al. 2017). Regardless of the causes of SK, the financial costs and emotional stress to cattlemen that are associated with these depredation events undermine predator conservation efforts (Naughton-Treves et al. 2003, Berger 2006, Muhly & Musiani 2009, Breck et al. 2011). We conclude that the importance of SK events should not be underestimated when designing strategies for puma conservation and puma–livestock conflict management and mitigation, particularly in areas where sheep and goat farming is a major economic activity.

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